

Surgical Approach to the Dolphin's Ear

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ABSTRACT A surgical approach to the cetacean (*Tursiops truncatus* and *Lagenorhynchus obliquidens*) ear represented a unique problem. The first obstacle was the development of a safe and humane anesthesia procedure and techniques of long-term physiological maintenance of the animal during surgery. The surgical anatomy was a challenge especially because of the extensive venous plexuses that invest the entire ear and adnexa. The *corpus cavernosum carotidis* and other small arterial networks course through this venous mass.

Sodium pentothal-halothane anesthesia and careful physiological monitoring were determined to be adequate for long-term maintenance during surgery and cochlear recording experiments. A specially designed surgical tank held the animal during the procedure. Immersion in water relieved the lungs of external pressure that ordinarily occurs, when the animal is out of the water, due to the flexible thorax. Thermoregulation was provided for by regulating the water temperature in response to the dolphin's core temperature. This arrangement also provided for underwater auditory stimulation and easy manipulation of the animal since dolphins with their lungs inflated are close to neutral buoyancy.

It was necessary to ligate the external and internal carotid arteries, neither of which supplies blood to the ear or brain. Hemostasis in the massive venous plexus could be achieved only by partial removal and subsequent application of oxycel and surgical cement to effectively dam off the area of the round window and other ear structures for electrical potential recording and experimental manipulations.

With this technique the round window of the cochlea was exposed. Fully anesthetized animals were maintained for periods up to 24 hours while electrophysiological measurements were being made. Some of the auditory measurements required further surgical manipulation of the auditory meatus, bulla, ossicular chain and other middle-ear structures.

Cetaceans lack an external ear or pinna, but it has been known for a long time that they can hear. Pindar, who lived from about 522 to 422 bc, claimed that dolphins could be attracted by a flute or lyre, and Aristotle was surprised that they fled from all kinds of noise despite their apparent lack of an auditory passage (Sljper, '58). Several theories have been put forward to explain how cetaceans hear. These vary widely, from the early suggestion of Camper (1787) that these animals hear only sounds produced in air and then only when the head is out of the water, to the more recent hypotheses of Norris ('68). Most of the theories of cetacean hearing have been treated in the additional works of Yamada ('53), Reysenbach de Haan ('58), Fraser and Purves ('60) and Dudok van Heel ('62).

Schevill and Lawrence ('53) reported that bottlenosed dolphins responded to frequencies above 100 kHz. Later Johnson ('66) produced the first detailed audiogram of a cetacean and showed that *Tursiops truncatus* had broad-band hearing extending to 150 kHz. Through these and numerous other investigations, it has been established that cetaceans have a keen sense of hearing. It was clear, however, that the theories of how the cetacean auditory mechanism worked had multiplied in the absence of detailed physiological and anatomical observations in the acoustic apparatus. Therefore, we set out to study auditory function in the living animal. The cochlear-potential method was chosen as

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the best means for a functional analysis of the physiological and anatomical mechanisms involved in dolphin hearing (McCormick et al., '70).

For this investigation, it was necessary to develop a surgical approach to the ear of two small cetaceans — the Atlantic bottlenosed dolphin (*Tursiops truncatus*) and the Pacific white-striped dolphin (*Lagenorhynchus obliquidens*). In 1964 when the first plans were made for these experiments, several obstacles were yet to be overcome before a long-term surgical procedure could be performed on dolphins. These included the following: (a) the development of techniques and physiological monitoring capabilities suitable for maintaining the animal in surgical anesthesia for periods of time up to 24 hours, (b) the development of a technique for holding the animal for long periods while the surgery was being done and the recordings made, (c) the determination of supportive steps necessary during the prolonged anesthesia and major surgical procedure, (d) the identification of anatomical landmarks of the surgical site and determination of the best surgical approach to the round window and middle ear.

Anesthesia and physiological monitoring

The anesthesia technique that was used for these experiments was the one described by Ridgway and McCormick ('67, '71).

No preanesthetic agents other than atropine (2 mg/100 kg) were given. Morphine appears to be more excitatory than depressive in dolphins (Ridgway, '65). Tranquilizers were avoided because of their detrimental effects on temperature regulation (Ridgway and McCormick, '71). This is especially important for dolphins under surgery for medical reasons since the animal must be placed back in the water to swim as soon as possible after an operation is completed if it is to have the best chances of survival. Drugs that produce peripheral vasodilatation directly or through ganglionic blockage or effects on the hypothalamus may produce a sharp drop in body temperature when the animal is returned to its pool. Water transports heat away from the submerged body over 20 times as fast as does air (Beckman, '63).

Thus drugs that cause peripheral vasodilatation also allow the body heat to flow rapidly into the water.

Induction of anesthesia was accomplished by the intravenous injection of 10–15 mg/kg of sodium thiopental in 2% solution. This rapidly relaxed the animal and halted respiration. The respiratory reflexes were always among the first to be depressed when a dolphin was anesthetized (Ridgway and McCormick, '71). The mouth could now be opened, the glottis pulled forward and downward from its normal intranarial position and an endotracheal tube inserted. Respiration was maintained by a Bird respirator with an apneustic plateau control device that enabled the machine to mimic the normal respiration of the dolphin. Thus the lungs were rapidly inflated, held inflated for 15–30 seconds and then deflated and rapidly filled again. The importance of this type of respirator rather than the standard human or animal machine should be emphasized.

The two species with which we worked (*Tursiops truncatus* and *Lagenorhynchus obliquidens*) exhibit some adaptations in pulmonary structure that are common to most odontocetes. These include: (a) a heavily armored cartilaginous but resilient branchial tree with cartilage extending right down to the alveoli, (b) muscular sphincters within the bronchi that appear capable of separating the lower bronchi into compartments, (c) thick alveolar walls that contain two rows of capillaries rather than just one, and (d) a large amount of elastic tissue. This pulmonary anatomy has been reviewed recently by Simpson and Gardner ('72).

These dolphins breathe two or three times each minute. Each breath is a deep one. The tidal air exchange is about 80% (Irving et al., '40). Cetaceans inhale actively and exhale passively as does man (Olsen et al., '69). However, passive exhalation of 80% of the lung air with each breath requires a great deal of elastic recoil by the lungs. The dolphin's flexible thorax collapses as pressure increases during a deep dive and the lungs must respond to the corresponding pressure changes as the pulmonary gas compresses and expands (Ridgway et al., '69). These factors probably account for the large amount of elastic tissue that the lungs contain. When

standard human or animal respirators are used, insufficient inflation time is achieved to permit adequate oxygenation of the blood. Although we have maintained one dolphin under surgical anesthesia using a standard respirator without an apneustic plateau, the arterial pO_2 slowly declined and could not be maintained at safe levels for over one hour without reinstituting an apneustic plateau.

After induction of anesthesia the heart beat, rather than following its normal respiratory arrhythmia, becomes steady at 80 to 120 beats per minute depending somewhat on the size of the animal (larger specimens having slower rates). Figure 1 shows the heart rate in a *T. truncatus* just before and just after pentothal administration. Preadnestic atropine was not given to this animal. As the barbiturate took effect, the heart rate increased to about 140 per minute, levelled off for a time, and then declined to a steady level of about 100 beats per minute.

As soon as endotracheal intubation was achieved 2% halothane was administered through a Fluotec vaporizer on the respirator. After two or three minutes at this

concentration, the halothane was reduced to about 1%. From this point on the halothane was regulated according to muscular reflexes, general physiological state, and the animal's heart rate. The heart rate tended to increase as the depth of anesthesia decreased. Frequency and depth of respiration were controlled in response to blood gas measurements taken at intervals of from 5 to 30 minutes from the central artery of the tail fluke or from one of the caudal arteries running along the tail stock.

The surgical tank

In our first series of experiments the animals were held on a stretcher suspended over and partly within a small tank of water. This was the method used for all previous dolphin surgery. The more prolonged of our earlier operations were abdominal surgical procedures in which the animal was placed on its back thus alleviating to a certain extent the pressure of body weight on the flexible rib cage. For ear surgery the animal had to be positioned on its side. We soon learned that the weight of the body imposed a serious

DOLPHIN HEART RATE

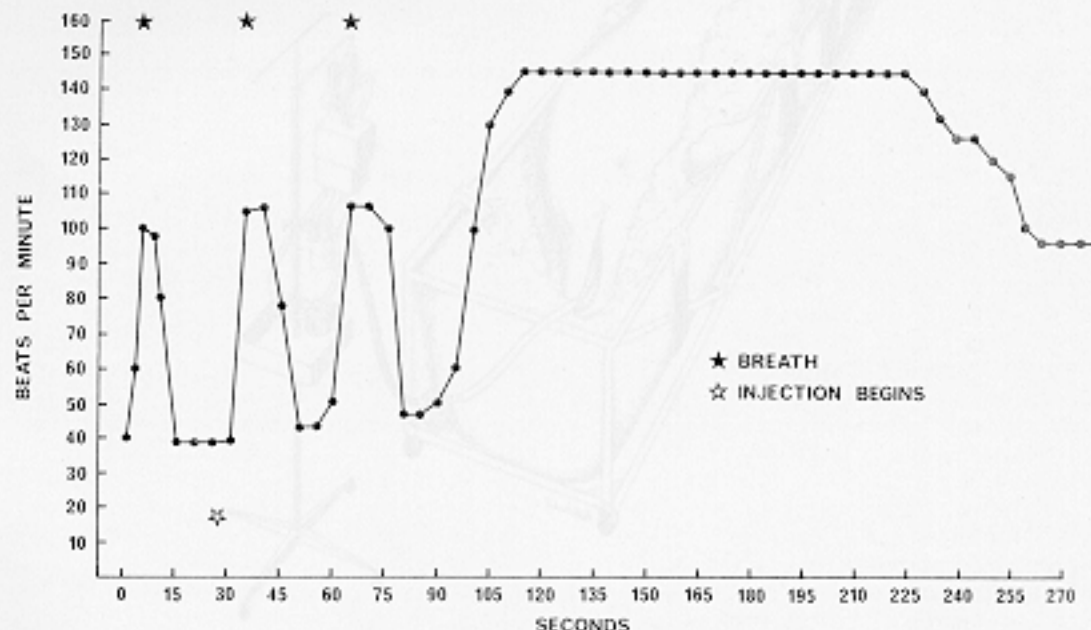


Fig. 1 The heart rate in a *Tursiops truncatus* is shown just before and just after intravenous injection of pentothal. Preadnestic atropine was not given to this animal.

load on the heart and lungs and hampered their action. This effect was evident after only a few hours, although we were able to maintain animals up to 20 hours in this manner.

Another method was developed so that the animal could be held suspended in water during the entire period of the operation and experimental session. For this we used a stainless steel tank 3 m \times 65 cm \times 90 cm (fig. 2). The dolphin was strapped on the standard stretcher (Ridgway and McCormick, '67) for induction of anesthesia. As soon as the animal was under anesthesia, it was transferred to the water-filled tank. In the tank it was suspended on soft padded straps, but since

the animal was almost entirely immersed very little weight rested on the straps. The temperature of the tank water was regulated in response to the dolphin's deep rectal temperature which was monitored constantly. In this surgical tank we maintained animals for up to 24 hours in an excellent physiological state. It appeared that these experiments could have proceeded considerably longer should it have been advantageous to do so.

Supportive procedures

Throughout the long period of anesthesia the heart action was monitored with an electrocardioscope (Electrodyne PMS-5). Body temperature was measured with a

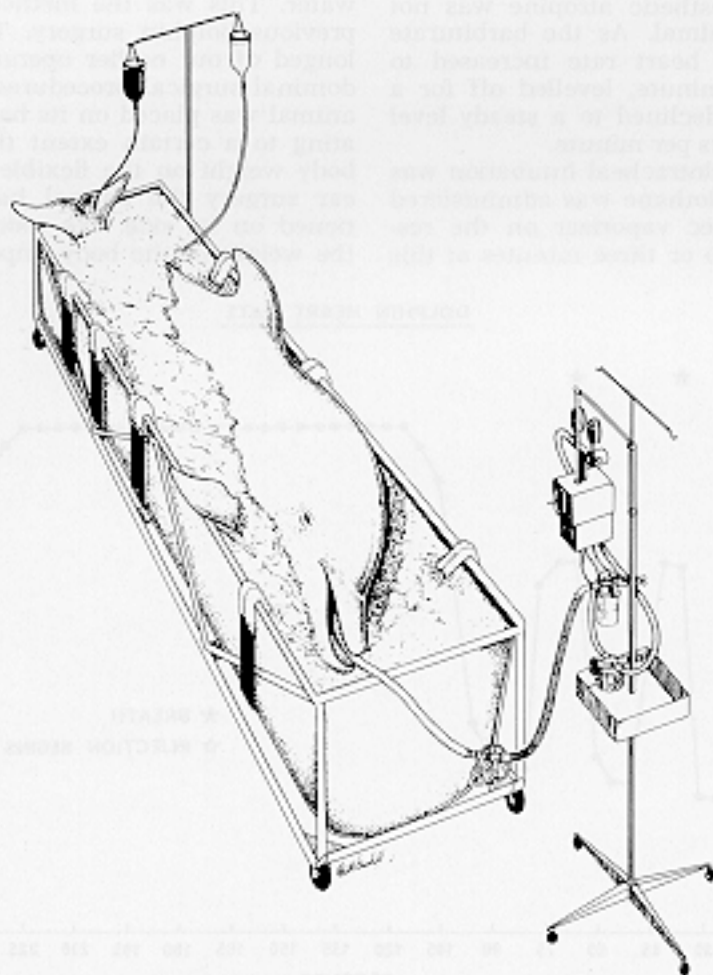


Fig. 2 This drawing shows the surgical tank with a dolphin in the customary position used for ear surgery. The Bird Mark 9 respirator with apneustic control unit is also shown.

thermistor probe inserted 25 cm into the rectum and maintained between 36.0 and 37.5° C. Venous and arterial blood samples were taken from the tail fluke at intervals of 15 to 30 minutes for determination of pO₂, pH, and pCO₂. Arterial values were maintained as follows: pO₂ 95–120 mmHg, pH 7.2–7.4, pCO₂ 30–45 mmHg. Arterial pressure and central venous pressure were monitored, and kidney perfusion was determined by measuring the urine output. Respiration and anesthetic administration were regulated by this constant check of physiological values.

Blood loss was unavoidable when a large portion of the massive plexus that surrounds the ear had to be removed to gain access to the round window. In a few instances transfusion was considered advisable. Differences in dolphin blood groups are of clinical significance (Myhre et al., '70). Therefore, it was necessary in advance of the operation to cross-match the blood of the prospective subject with blood from other dolphins in our colony. Suitable donors were selected and two or three liters of compatible blood were kept on hand for transfusion.

From time to time recording sessions were interrupted by involuntary contraction of certain muscle groups. When this occurred, after six to eight hours of anesthesia after recording had begun, we administered intravenous Flaxedil (gallamine). This caused muscular relaxation for about 90 minutes.

Intravascular fixation and latex injection technique

The initial dissections for working out a surgical approach were carried out on several specimens of *T. truncatus* and one of *L. obliquidens* that were obtained from various oceanaria in California or Florida. In all of these cases the animals had died from natural causes. We were able to obtain enough of these specimens to work out an approach for our first surgical procedure on a live animal. For assistance in dissection and identification of parts we referred to the papers of Murie (1874), Boenninghaus ('04), Burne ('52), Lawrence and Schevill ('65), and Galliano et al. ('66).

One fresh carcass, a 150-kg female *T. truncatus*, was perfused with latex injected intravascularly. The thorax was opened and a large cannula was placed in the aorta pointing cephalad. Two cannulae, one directed caudad and the other cephalad, were placed both in the external carotid and in the external jugular vein. Perfusion fluid was pumped alternately through the two carotid cannulae and the aortic cannula. The jugular cannulae provided drainage. After the vascular system had been washed with 60 liters of Ringer's solution, 120 liters of 10% formalin were pumped through. The arteries were then injected with 4 liters of pink latex and the venous system was injected with 5 liters of blue latex administered through the jugular vein. The animal was placed in a large formalin-filled tank for dissection

Abbreviations

AExC, external carotid artery (with surrounding venous plexus)	Mand, mandible	Per, periotic bone
AIC, internal carotid artery	MCA, cervicalis ascendens, muscle	Ptp, pterygoid plexus within pterygoid sinus
AVP, arteriovenous plexus	MD, deltoid muscle	RW, round window from which cochlear potentials were recorded
B, blubber (hypodermis)	MIH, interhyoid muscle	Sig, sigmoid process
CA, auricular cartilage	MMH, mastohumeral muscle	SpExo (Fig. 6), styloid process of the exoccipital bone with the ventral posterior margin partially rongueured away
Cb, cerebellum	MO, occipital muscle	SpExo (Fig. 7), styloid process of the exoccipital bone with the ventral posterior margin rongueured away
CTph (Fig. 5), tympanohyal cartilage	MPc, panniculus carnosus muscle	Tb, tympanic bone
CTph (Fig. 6), remains of the tympanohyal cartilage	MSc, scalenus muscle	V, veins
EAM, external auditory meatus	MSb, sternohyoid muscle	VII, internal jugular vein note that branches of the internal jugular vein commu- nicate with the plexus around the external carotid artery
EMB, entrance point of external meatus into tympanic bulla	MSM, sternomastoid muscle	
EpITb, external posterior lobe of the tympanic bone	N, nerves	
ExJ, external jugular vein	N2, optic nerve	
FC, frontal cortex	N5, trigeminal nerve	
IO, inferior olive	N8, auditory nerve	
LN, lymph nodes	N9, glossopharyngeal nerve	
MA, auricular muscles	N10, vagus nerve	
	N11, spinal accessory nerve	
	N12, hypoglossal nerve	
	P, pituitary	
	PRp, peribullar plexus	

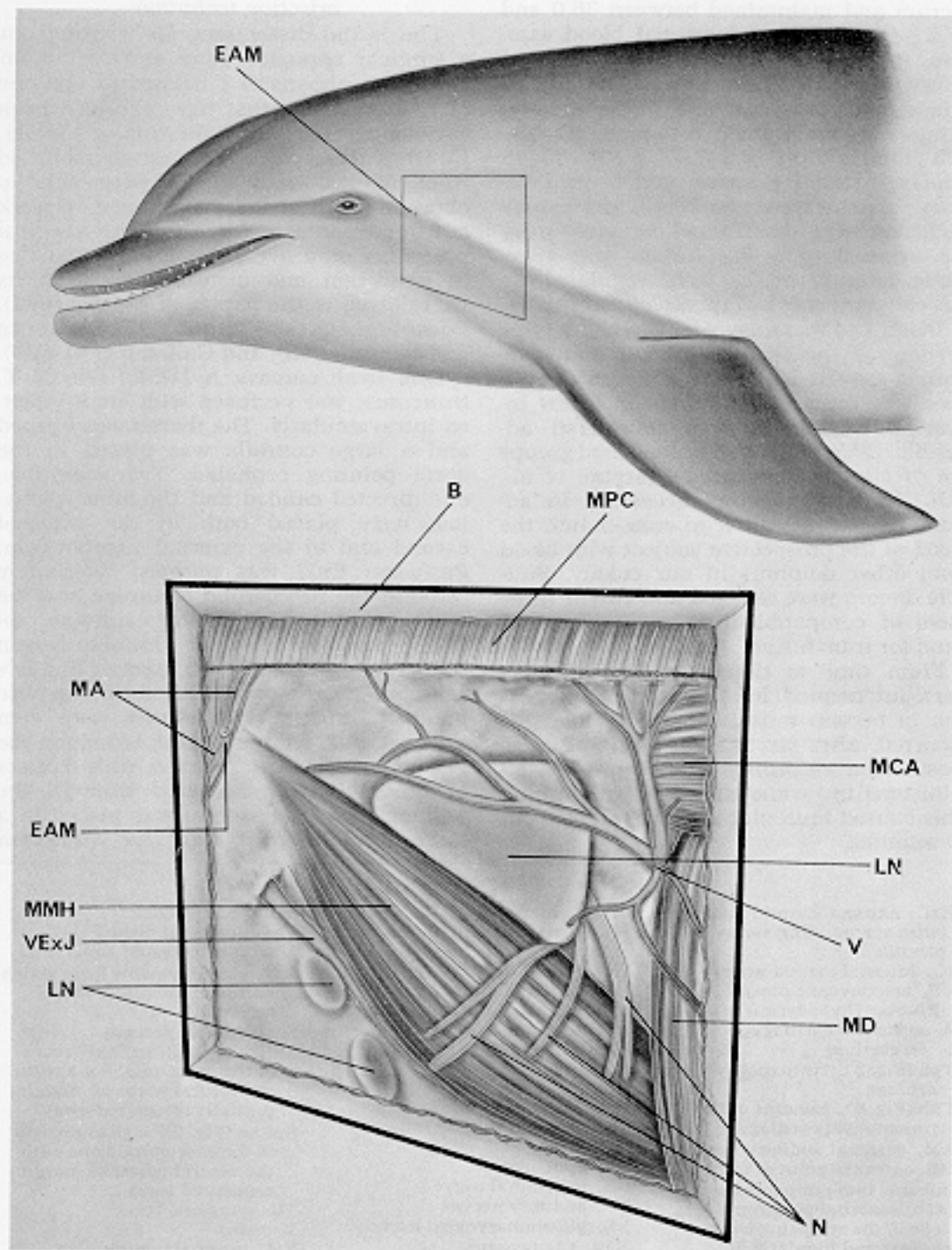


Fig. 3 The site of surgical incision is illustrated above and a view of the left side of the head with the skin, blubber, fascia, and superficial musculature removed appears below.

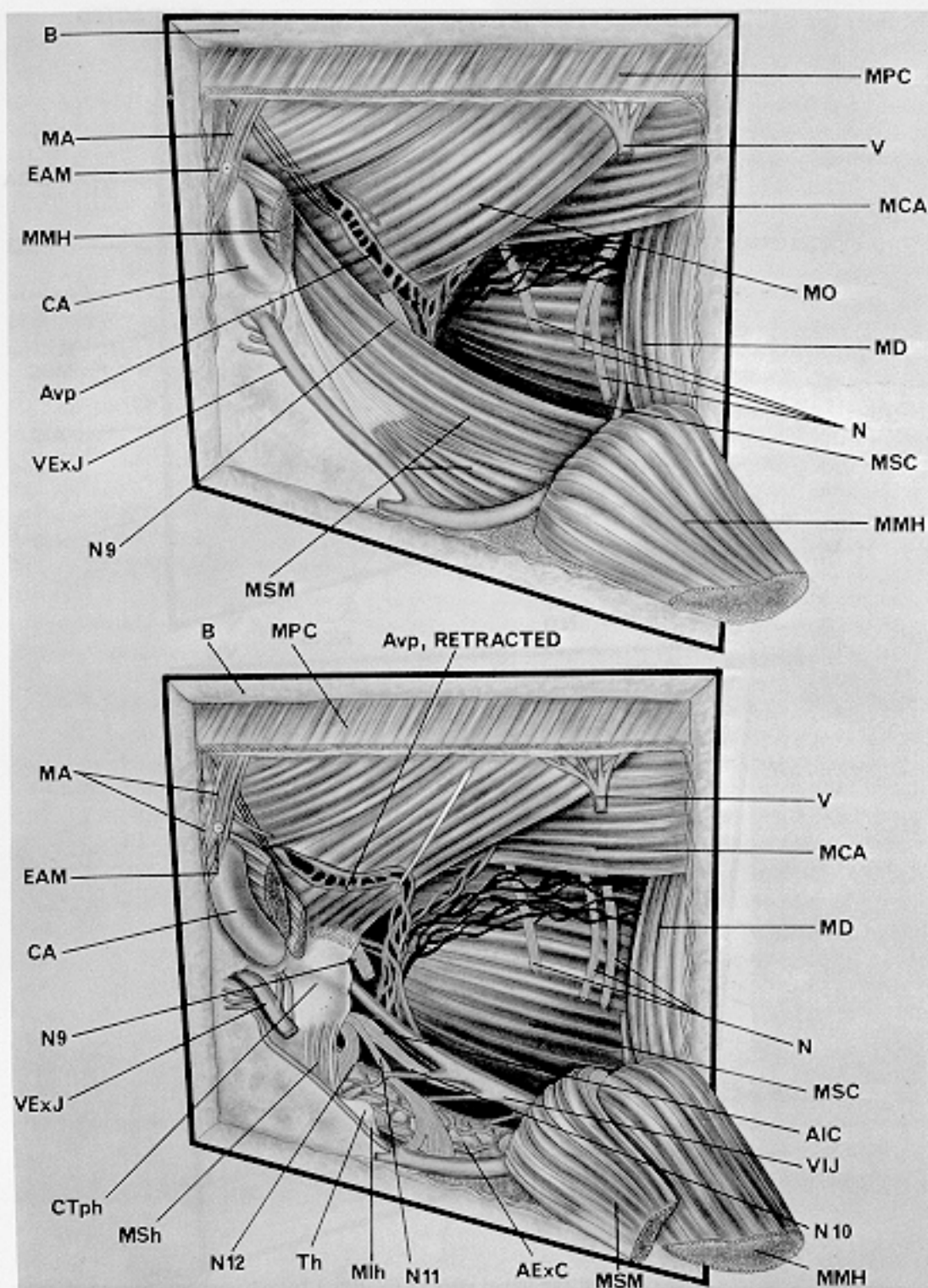


Fig. 4 Progress of the surgery is depicted. The vestige of the pinna is on the left; the jugular vein and the large muscles are transected.

Fig. 5 The exposed styloid process is depicted in its articulation with the hyoid bone which overlays the ear bones.

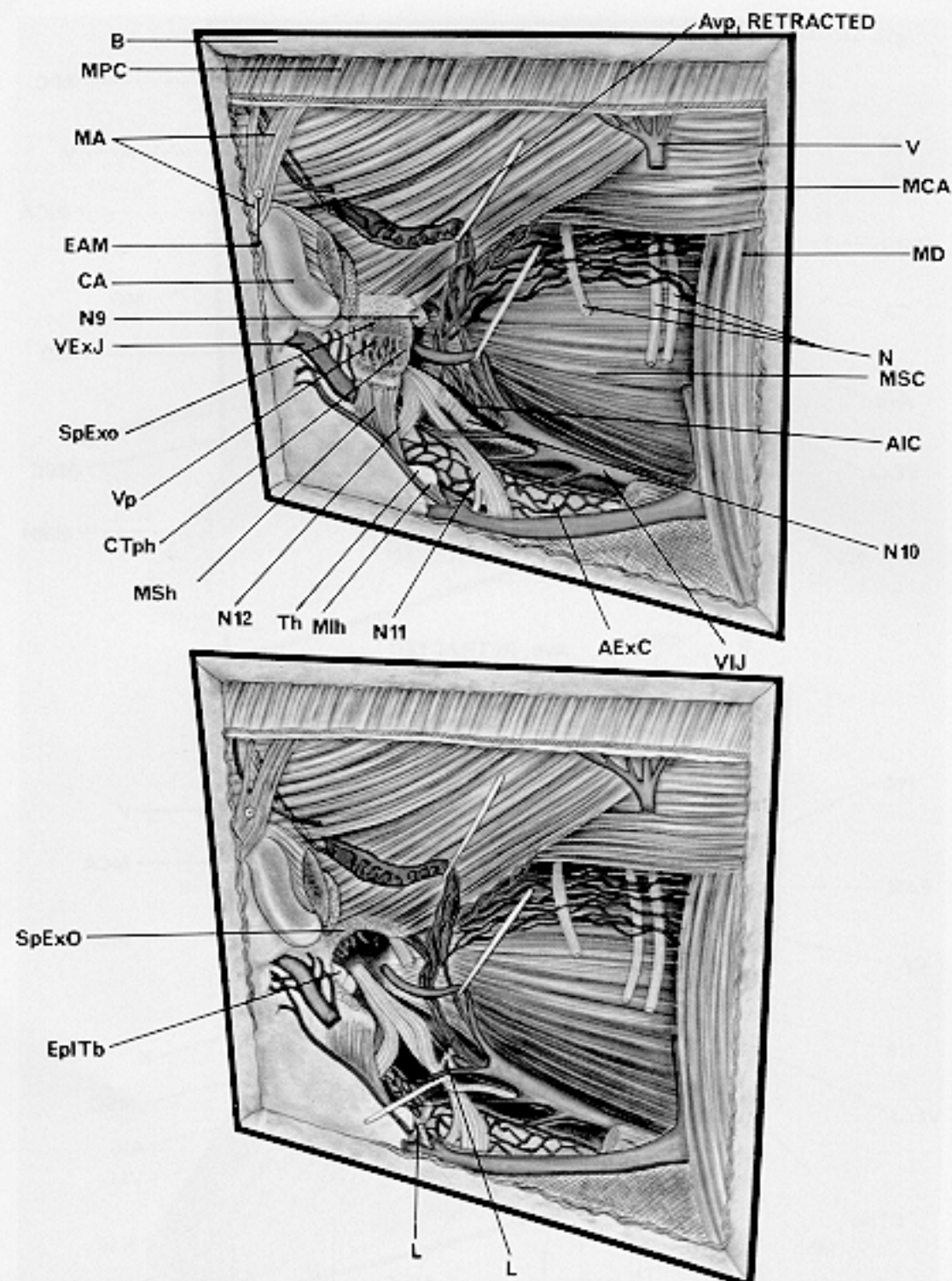


Fig. 6 The stylomastoid process and the upper edge of the hyoid bone have been rongeured away exposing the veins (VP) of the retial network that surround the ear bones.

Fig. 7 The ear bones are exposed after the external and internal arteries are tied off (L). The internal carotid artery must be dissected out of the sheath of the vagus nerve. The internal carotid artery supplies the corpus cavernosum that runs through the area and probably expands to protect some of the air sinuses from collapse during deep dives.

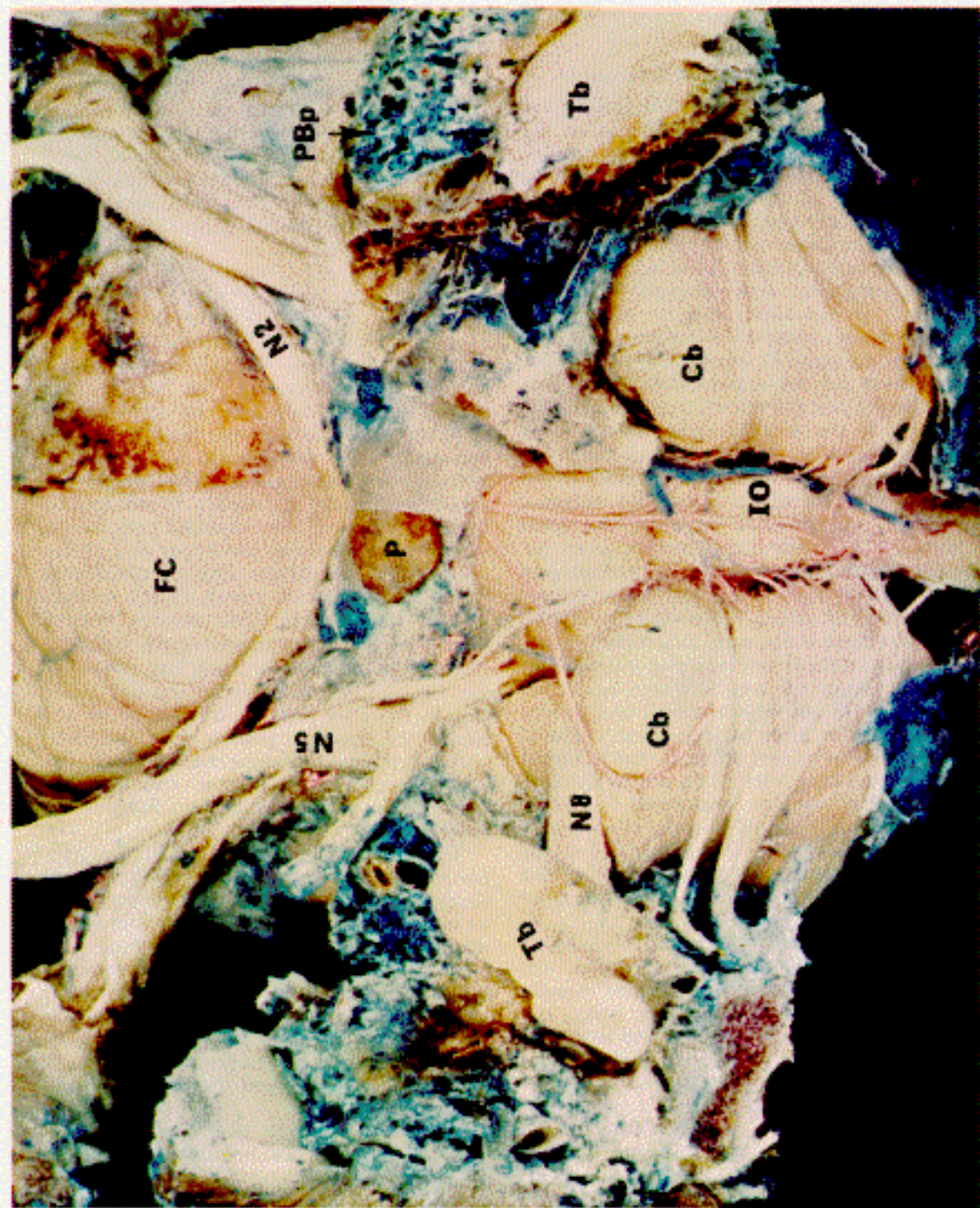


Fig. 8 This photograph shows the partly dissected underside of the cranial vault of the latex injected *T. truncatus*.

after the latex had hardened. Figures 3 through 9 were developed primarily from dissections of this animal.

Description of the actual surgery

Normally, the animal was positioned with its left side down as shown in figure 2. However, some of the operations were done on the opposite side. As shown in figure 3, an incision was made from above the external auditory meatus to the anterior insertion of the flipper, and the skin and blubber (epidermis, dermis, and hypodermis) were removed. The superficial *M. panniculus carnosus* and its fascia were also removed from the area. This exposed the large *M. mastohumeralis* which runs from the mastoid process of the temporal bone just dorsomedial to the auditory meatus to the medial aspect of the head of the humerus. A large lymph node lies dorsal to the muscle and two smaller nodes lie on its ventral margin. The external jugular vein courses between the most cephalad of these small nodes, goes beneath the *M. mastohumeralis*, and crosses between this muscle and the large *M. sternomastoideus* beneath. Nerves crossing the *M. mastohumeralis* were transected as the muscle was dissected free and cut near its cephalic insertion and reflected back, exposing the *M. sternomastoideus* and the external jugular vein. Arteries and veins of the muscle were tied off as it was reflected (fig. 5) and care was taken not to damage the external jugular vein since it crosses the ventral surface of *M. mastohumeralis*. We frequently used the external jugular vein for drawing blood samples or for passing a catheter for the monitoring of central venous pressure.

The *M. sternomastoideus* was clamped near its cephalad insertion and cut. Reflection of this large double-headed muscle exposed the internal jugular vein, the external carotid artery, and the articulation between the hyoid bone and the styloid process at the tympanohyal cartilage. The external carotid artery is large and is surrounded by a venous plexus which communicates freely with the internal jugular vein which lies dorsomedial to it. The *N. hypoglossus* and *N. accessorius* cross just caudad to the tympanohyal cartilage and go laterally between the inter-

nal jugular vein and the carotid artery. The *N. vagus* emerges with the former nerves, but continues in a caudad direction just medial to the internal jugular vein. The small carotid artery lies adjacent to and just medial to the vagus nerve.

About two centimeters of the ventral margin of the styloid process was then rongeuired away (fig. 6). This was done carefully with the assistance of periosteal elevators so that the internal periosteum was preserved intact with the massive venous plexus behind it.

The vagus nerve was gently dissected away from the internal carotid artery (fig. 7) and the artery tied off with umbilical tape. The external carotid artery was also tied. The internal carotid supplies the *corpus cavernosum* of the middle ear (Boenninghaus, '04) and the external carotid supplies much of the head including various smaller arteries in the cephalad portion of the surgical site. Neither of the carotids appears to supply blood to the brain or cochlea. The exposed periosteum was cut away as was the upper end of the tympanohyal cartilage. This cartilage was removed along with much of the venous plexus underneath. This venous system is extensive and interconnected with the venous plexuses of the eyes and the other ear by way of the ventral cranial vault (fig. 8), so that hemostasis cannot be obtained by ligating vessels. We therefore had to construct a dam and seal off the surgical area with oxycel and surgical cement (Isobutyl, Ethicon, Inc., Somerville, New Jersey).

The external posterior lobe of the tympanic bone was exposed (fig. 7) and more supporting fibrous tissue and venous plexus were removed gradually until the round window of the petrous (periotic) bone was exposed (figs. 9, 10). Figure 9 shows the relationship of the ear bones to the carotid arteries, auditory meatus (and auricular cartilages), *N. vagus*, *N. hypoglossus*, *N. glossopharyngeus*, *N. accessorius*, the massive venous plexus, and the posterior margin of the mandible.

After an electrode was placed on the round window of the cochlea and electrophysiological recording started, the experimental program often called for surgical interference with various structures associated with the auditory apparatus. The

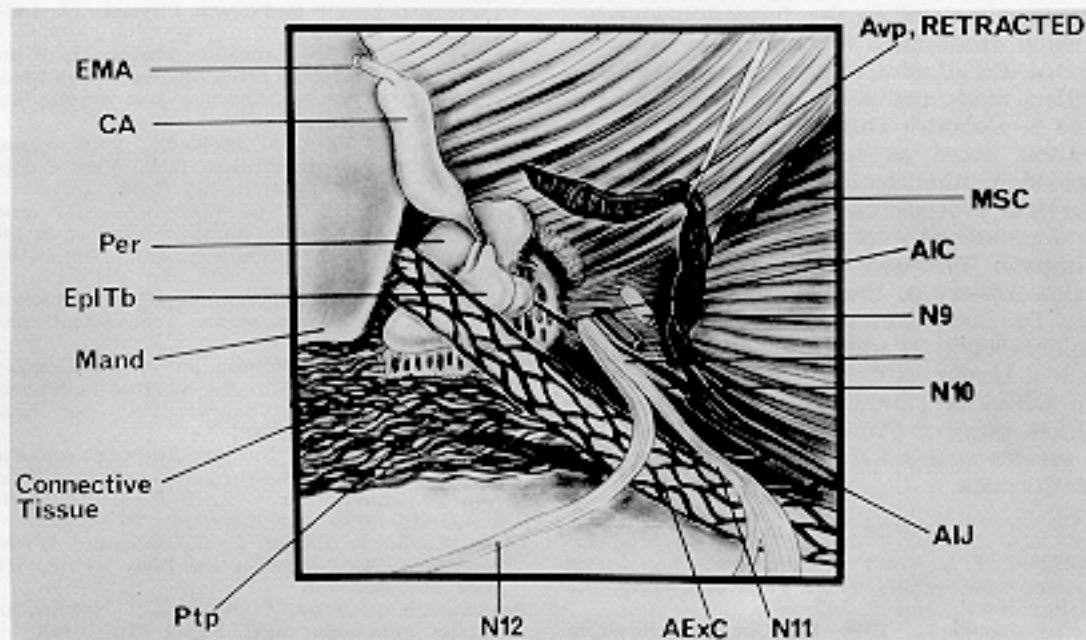


Fig. 9 This drawing shows a lateral view of the surgical site with the ear bones exposed.

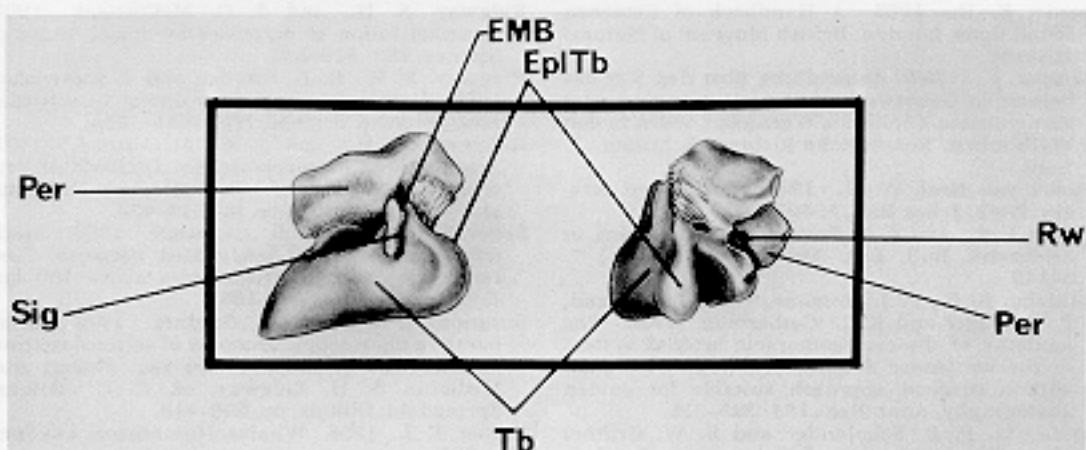


Fig. 10 This drawing illustrates the isolated left ear bones of a *T. truncatus* with the lateral view on the left and the posterior view on the right.

external auditory meatus was bisected in several places, from just beneath the epidermis to its point of entry into the auditory bulla. In one test the tympanic conus and tympanic membrane were removed. In each of several animals the auditory bulla was opened carefully with small rongeurs. This exposure gave access to the bones, muscles, and ligaments of the middle ear. Experiments called for the application of tension to parts of the ossic-

ular chain and excision of various structures so that their relative importance in the hearing process could be assessed. The results of these experiments have been described in a previous report (McCormick et al., '70).

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LITERATURE CITED

- Beckman, E. L. 1963 Thermal protection during immersion in cold water. Proc. 2nd Symp. Underwater Physiol., 2: 247-266.
- Boenninghaus, G. 1904 Das Ohr des Zahnwales, zugleich ein Beitrag zur Theorie der Schalleitung. Zool. Jahrb. Abt. Anat. Ontog., 19: 189-360.
- Burne, R. H. 1952 A Handbook of Cetacean Dissections. London, British Museum of Natural History.
- Camper, P. 1787 Abhandlung über den Sitz des beinernen Gehörwerkzeugs und über einen der vornehmsten Theile des Werkzeugs selbst in den Wallfischen. Sammtliche kleinere Schriften, 2: 1-40.
- Dudok van Heel, W. H. 1962 Sound and cetacea. Neth. J. Sea Res., 1: 407-507.
- Fraser, F. C., and P. E. Purves 1960 Hearing in cetaceans. Bull. Brit. Museum Nat. Hist., 7: 3-140.
- Galliano, R. E., P. J. Morgane, W. L. McFarland, E. L. Nagel and R. L. Catherman 1966 The anatomy of the cervicothoracic arterial system in the bottlenose dolphin (*Tursiops truncatus*) with a surgical approach suitable for guided angiography. Anat. Rec., 155: 325-338.
- Irving, L., P. F. Scholander and S. W. Grinnell 1941 The respiration of the porpoise *Tursiops truncatus*. J. Cell. and Comp. Physiol., 17: 145-168.
- Johnson, C. S. 1966 Auditory Thresholds of the Bottlenosed Porpoise (*Tursiops truncatus* Montagu). U. S. Naval Ordnance Test Station Report T.P. 4178, 28 pp.
- Lawrence, B., and W. E. Schevill 1965 Gular musculature in delphinids. Bull. Mus. Comp. Zool., Harvard University, 133: 5-58.
- McCormick, J. G., E. G. Wever, J. Palin and S. H. Ridgway 1970 Sound conduction in the dolphin ear. J. Acoustical Soc. Amer., 48: 1418-1428.
- Murie, J. 1874 On the organization of the caaing whale, *Globicephalus melas*. Trans. Zool. Soc. London, 8: 235-301.
- Myhre, B. A., J. G. Simpson and S. H. Ridgway 1971 Blood groups in the Atlantic bottlenose porpoise (*Tursiops truncatus*). Proc. Soc. Exp. Biol. Med., 137: 404-407.
- Norris, K. S. 1968 The evolution of acoustic mechanisms in odontocete cetaceans. In: Evolution and Environment. E. T. Durke, ed. Yale University Press, New Haven, pp. 297-324.
- Olsen, C. R., R. Elsner, F. C. Hale and D. W. Kenney 1969 Blow of the pilot whale. Science, 163: 953-955.
- Reysenbach de Haan, F. W. 1958 Hearing in whales. Acta otolaryngol., Suppl. 134: 1-114.
- Ridgway, S. H. 1965 Medical care of marine animals. J. Amer. Vet. Med. Assoc., 147: 1077-1085.
- Ridgway, S. H., and J. G. McCormick 1967 Anesthetization of porpoises for major surgery. Science, 159: 510-512.
- Ridgway, S. H., B. L. Seronice and J. Kanwisher 1969 Respiration and deep diving in a bottlenose porpoise. Science, 166: 1651-1654.
- Ridgway, S. H., and J. G. McCormick 1971 Anesthesia of the porpoise. In: Textbook of Veterinary Anesthesia. L. R. Soma, ed. Williams and Wilkins, Baltimore, pp. 394-403.
- Schevill, W. E., and B. Lawrence 1953 Auditory response of a bottlenosed porpoise, *Tursiops truncatus*, to frequencies above 100 kc. J. Exp. Zool., 124: 147-165.
- Simpson, J. G., and M. Gardner 1972 Comparative microscopic anatomy of selected marine animals. In: Mammals of the Sea: Biology and Medicine. S. H. Ridgway, ed. C. C. Thomas, Springfield, Illinois, pp. 298-418.
- Slijper, E. J. 1958 Whales. Hutchinson, London, p. 203.